USE OF RESTORED GRASSLANDS BY MAMMALS IN A DYNAMIC AGROECOSYSTEM: INSIGHTS FROM CAMERA TRAPPING

BY

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THESIS

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ABSTRACT

Habitat loss is one of the leading causes of endangerment for terrestrial vertebrates. For instance, 99.9% of the tallgrass prairie has been lost in Illinois. Restoration programs such as the Conservation Reserve Program (CRP) and State Acres for Wildlife Enhancement (SAFE) were created in part to ameliorate grassland loss. Previous assessments of responses of mammals to grassland restoration efforts have not focused on medium to large sized species because of sampling difficulties. More generally, few assessments of restoration outcomes consider effects of landscape context. I integrated camera trapping with occupancy modeling for two seasons (summer and winter) to assess mammal responses on 30 restored grassland sites in a dynamic agroecosystem in Illinois from 2014 to 2015. I tested hypotheses about the effects of local habitat conditions and landscape context on use of restored grasslands by four focal species: raccoons (*Procyon lotor*), eastern cottontails (*Sylvilagus floridanus*), coyotes (*Canis latrans*), and white-tailed deer (*Odocoileus virginianus*). Most species showed seasonal differences in grassland use that reflected the dynamic nature of the surrounding agricultural matrix (i.e., loss of hiding cover and supplemental food due to crop harvesting). Overall, landscape context was important in determining use of created grasslands. For instance, distance to nearest forest was the main predictor of site occupancy for raccoons, which has management implications regarding future site enrollment to reduce predation on grassland songbird nests. The red fox (*Vulpes vulpes*) was not detected on any site despite >5,000 camera nights of sampling, which points to the need for further monitoring to determine the status of this small canid in non-urban areas of the Midwest. Grasslands created by the CRP and SAFE programs provide habitat for medium and large mammals, but use of these habitats strongly depends on the temporally dynamic matrix and landscape context.

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INTRODUCTION

Habitat loss is one of the leading causes of endangerment for terrestrial vertebrates (IUCN 2014). In Illinois, like many states in the Midwestern U.S., the landscape is now dominated by intensive, row-crop agriculture (Warner 1994, Mankin and Warner 1997). In fact, 99.9% of tallgrass prairie has been lost due to this land conversion (Howe 1994, Samson and Knopf 1994). In response, programs have been initiated to ameliorate habitat loss by providing incentives for people to create habitat for native species. For example, the Conservation Reserve Program (CRP), and the newer initiative State Acres for Wildlife Enhancement (SAFE), have created new grasslands on former croplands. These programs encourage farmers to enroll for 10-15 year intervals in exchange for financial incentives. Due to the dominance of agriculture and nature of voluntary enrollment, however, the landscape is a patchwork of habitat embedded in a matrix of cropland.

Mammals are ecologically important organisms in grassland ecosystems because of their significant roles in trophic interactions, both as predators and prey. Herbivores also can influence vegetative communities through their foraging activities and thus may affect restoration outcomes. Some mammal species are also valued by the public as game species. The agricultural matrix could affect use of restored grasslands by mammals in two main ways. First, crop fields could serve as supplemental habitats providing food (Dunning et al. 1992), especially during the growing season (Beasley et al. 2006, Colligan et al. 2011). Second, the agricultural matrix could provide cover and affect movements to restored grasslands from other landscape elements (e.g., forests; Grovenburg et al. 2010). This connectivity provided by agricultural fields is temporally dynamic due to the annual planting and harvesting of crops (Cosentino et al. 2011).

In particular, harvesting produces a rapid, stark change that may inhibit the movements of many species through the agricultural matrix.

Other landscape variables also may affect use of restored grasslands by mammals. Some restoration sites may be too small to support populations of mammal species dependent on grassland habitat, and occurrence of these species may require movements among grassland patches. Other mammals that use restored grasslands may depend on resources provided by additional habitats such as forest or water. A species use of a grassland may therefore be contingent on proximity to other critical habitats, and the ability of the species to move through the agricultural matrix. Hence, landscape context should be considered when evaluating programs like SAFE and CRP. However, landscape context is rarely included in assessments of ecological restoration (Brudvig 2011; but see Mulligan et al. 2013 and Cosentino et al. 2014 for examples with mammals).

Despite the integral role of medium to large mammals in grasslands, past monitoring of ecological restorations has focused on small mammals because they are easier to sample via livetrapping (Stone 2007, Richardson 2010, Mulligan et al. 2013, DeGolier et al. 2015). Now, non-invasive survey methods such as camera trapping are providing an effective way to monitor habitat use of larger mammals (Long et al. 2008, Rowcliffe and Carbone 2008, Burton et al. 2015). Data from camera traps can be integrated with occupancy modeling to obtain unbiased estimates of site use despite imperfect detection of species (Cove et al. 2012, Kalle et al. 2014, Robinson et al. 2014). Although camera trapping is now widely used for monitoring mammals, it has only recently been applied to assess restoration outcomes (Derugin et al. 2016).

I employed camera trapping to evaluate how medium and large mammals used restored grasslands during summer and winter in a dynamic agroecosystem in Illinois. I focused on

effects of patch size, vegetation cover, and landscape context because these variables can be managed through selective enrollment when creating new grassland habitats. I documented all resident mammals using the grasslands, and then had adequate data to conduct statistical analysis for four species: raccoon (*Procyon lotor*), eastern cottontail (*Sylvilagus floridanus*), coyote (*Canis latrans*), and white-tailed deer (*Odocoileus virginianus*).

Raccoons are generalist mesocarnivores that function as important scavengers (DeVault et al. 2011) and nest predators (Heske et al. 1999, Rodewald and Kerns 2011, Friesen et al. 2013) including of grassland birds (Renfrew and Ribic 2003, Lyons et al. 2015). Hence, any factors that affect use of restored grasslands by raccoons could be consequential to nest predation rates for declining bird species (e.g., Schmidt 2003). Lagomorphs such as eastern cottontails are herbivores that can strongly affect vegetation composition due to preferential foraging (Barrio et al. 2012, Rebollo et al. 2013). Eastern cottontails are a prey species for many predators including coyotes (Phillips and Hubert 1980, Morey et al. 2007) and they prefer thick cover (Althoff et al. 1997, Bock 2006). Cottontails are also a game species that exhibited regional declines in Illinois coincident with intensification of agriculture (Mankin and Warner 1999a). Coyotes have expanded their geographic range over time (Prugh et al. 2009) and are now the top predators in many regions (Gompper 2002, Crimmins et al. 2012). Coyotes can displace smaller canids such as red foxes (*Vulpes vulpes*; Gosselink et al. 2003) due to intraguild predation (Palomares and Caro 1999, Robinson et al. 2014), which can trigger trophic cascades (Roemer et al. 2009). The white-tailed deer is the largest herbivore in Midwestern grassland ecosystems where it can affect plant species composition and the tempo of succession (Batzli and DeJaco 2013). White-tailed deer are also an economically important game species (Illinois Department of Natural Resources 2015).

I tested the following predictions for my four focal species: 1) Raccoons use diverse habitats but are typically associated with forest (Beasley et al. 2006, 2011), particularly for denning, and with water (Gehrt and Fritzell 1998, Beasley and Rhodes 2010). Therefore, I predicted that use of grassland restorations by raccoons would be positively associated with their proximity to forest and to ponds and streams. 2) Because crops can provide cover that should encourage movements across crop fields, I expected use of grasslands by raccoons to be greater during summer. 3) If areas with more extensive grasslands promote movement through the agricultural matrix, and especially provide alternate cover when crops are absent, I expected greater use of more connected sites (near other grasslands) by raccoons during winter. 4) In my restored grasslands, cool-season grasses consistently provide dense cover, whereas warm-season grasses provide more patchy cover (Berry, pers. obs.). If cottontails prefer dense vegetation because it provides hiding cover and reduces predation risk, then there should be a positive correlation between the probability of site occupancy and dominance of cool-season grasses. 5) I expect that cottontails perceive the open agricultural matrix as risky during winter, whereas restored grasslands could serve as refuges as they provide food and cover after crops are removed. If cottontails constrict their use of agricultural fields after crop harvest, occupancy probabilities on grasslands should increase from summer to winter. 6) If coyotes seek patches where their lagomorph prey are abundant (Ariaz-Del Razo et al. 2012), then I would expect a pattern of co-occurrence among sites for coyotes and cottontails, and increased use of restored grasslands by coyotes in winter. 7) Coyotes generally avoid interactions with humans (Gosselink et al. 2003, Magle et al. 2014). Thus, I expect an inverse relationship between site occupancy for coyotes and distance to nearest human structure. 8) White-tailed deer in Illinois favor early successional upland forest (Nixon et al. 1991), so I predict that grassland occupancy by deer

should be positively related to proximity to nearest forest. 9) Because deer fawns are at risk of predation by coyotes and other predators, denser hiding cover should be preferred during summer when fawns are present. Thus, I expect higher occupancy during summer for sites dominated by cool-season grasses.

METHODS

Study Area

My 30 study sites were grasslands located in central Illinois in the Grand Prairie and Southern Till Plain Natural Divisions (Fig. 1). These grassland sites were a mixture of parcels in the State Acres for Wildlife Enhancement (SAFE) Program (see Mulligan et al. 2013) and the Conservation Reserve Program (CRP). The sites were representative of these habitat programs in my region in terms of variation in size, landscape context, and vegetation cover. The 30 sites ranged from 1 to 256 ha (mean = 37 ha). The sites were all established grasslands seeded ≥3 years prior to sampling. Central Illinois is dominated by intensive agricultural production (Mankin and Warner 1997). For instance, about 80% of the land in the Grand Prairie Region is planted with annual row crops (corn or soybean; Schooley et al. 2012). My grassland sites were embedded in this agricultural landscape.

My SAFE and CRP sites were seeded with dominant grasses that I classified into three categories: cool-season grasses (10 sites), warm-season grasses (12 sites), or a mix (8 sites). I classified the sites by visually estimating the dominant grass species at each of four camera quadrants (see below) as either cool-season or warm-season. If ≥3 quadrants were dominated by warm- or cool-season grasses, then the plot received that designation. Otherwise, sites were considered as mixed. The common cool-season species were smooth brome (*Bromus inermis*), Virginia wild rye (*Elymus virginicus*), and Canada wild rye (*E. canadensis*); whereas the common warm-season species were big bluestem (*Andropogon gerardi*), little bluestem (*Schizachyrium scoparium*), switchgrass (*Panicum virgatum*), side oats (*Bouteloua curtipendula*), eastern gamagrass (*Tripsacum dactyloides*), and Indian grass (*Sorghastrum nutans*).

Sampling with Camera Traps

I sampled mammals with camera traps on the 30 sites during two seasons, "summer" (June 2014 – October 2014) and "winter" (November 2014 - March 2015), which corresponded to the growing and non-growing seasons for agricultural crops (Mankin and Warner 1999b). Within each season, I sampled each site for 28 consecutive days (Magle et al. 2014). I was able to sample 10 sites at one time, so sites were placed into three groups for sampling within a season based on logistical considerations.

I sampled each site with four trail cameras (Bushnell Trophy Cam, Model 119436c; Magle et al. 2014, DaVanon et al. 2016) after splitting sites into four quadrants and placing the camera near the center of each. The cameras have an infrared motion sensor and a flash for taking photographs at night. I set the cameras to take three-shot bursts with a 10-second trigger delay after activation. The cameras were placed 150 cm above the ground by mounting them on fence posts. Cameras were pointed down toward a bait post (3.4 m away) at an angle of 45 degrees to reduce false triggers caused by the moving vegetation in the background. I cleared vegetation from a 6.3-m^2 area centered on the bait post to reduce false triggers further. The bait post was placed north of the camera to avoid solar interference. Bait posts consisted of a punctured can of cat food (salmon flavor) and a fatty acid tablet (Wildlife Control Supplies; Magle et al. 2014) in wire mesh. The bait was intended to attract nearby mesocarnivores, but herbivores might also have been curious about the strong scent. I visited all cameras two weeks after deployment to check the status of the batteries and memory usage.

I stored photographs from the cameras according to the protocol by Harris et al. (2010), and categorized photographs using the protocol by Sanderson and Harris (2013). The resulting

output from each site included an occupancy matrix plus the number of independent photographs (>60 min apart) for my focal species.

Environmental Covariates

I measured covariates that could be relevant either for detection or occupancy (MacKenzie et al. 2006) for the focal species (Table 1). I considered two factors that could affect the probability that a species would be photographed given it was present at the site: patch size and sampling effort. Patch size (ha) was measured as the continuous area of grassland delimited by maintained breaks, roads, or other habitat. Because each site had four cameras (one in each quadrant) regardless of its total area, larger sites might be less thoroughly sampled than smaller sites, and species might have a greater probability of being missed. Patch size was ln-transformed prior to analysis. Sampling effort equaled the number of days that cameras were active during a sampling season. The maximum was 28 days, but some cameras were active for fewer days due to failure (summer: mean = 25.98 days, SE = 0.36; winter: mean = 24.25 days, SE = 0.47). Although variation in sampling effort among sites was small, sites where cameras were operating for a greater number of days might have had a higher probability of detecting less common species. Patch size and sampling effort were deemed potentially important detection covariates for all species.

Occupancy covariates included patch size, vegetation type, distance to nearest other grassland (measure of patch isolation), and distances to nearest forest, human structure, stream, and pond (Table 1). Vegetation was an ordinal variable that indicated the dominant vegetation at a site was cool-season grasses (1), mixed (2), or warm-season grasses (3). The other occupancy covariates assessed landscape context and were measured as linear distances (m) from focal

grasslands to other features (edge-to-edge distances). I measured these landscape covariates from digital orthophotos with ArcMap (ver. 10.3) and Google Earth (ver. 7.1.5.1557). A forest was classified as a stand of trees and excluded linear rows of trees. Distances to forest, human structure, stream, and pond were ln-transformed. Because the covariates 'patch size' and 'distance to nearest grassland' exhibited multicollinearity (r = 0.66), I used Principal Components Analysis (PCA; PRINCOMP Procedure, SAS Institute Inc. 2013) to create orthogonal principal components. The first axis (Size_Iso) accounted for 83% of the variation and was positively correlated with patch size (r = 0.91) and distance to grassland (r = 0.91). Size_Iso represented a gradient from small, connected grasslands to large, isolated grasslands.

I also wanted to determine if presence of a predator (coyote) affected presence of its prey (eastern cottontail), and the reverse, beyond effects of other occupancy covariates. To do this, I used the conditional occupancy probability from the most supported occupancy model based on habitat and landscape covariates for each species (see next section).

Occupancy Modeling

Occupancy modeling is a proven method for using presence-absence data to assess habitat relationships while accounting for false absences (MacKenzie et al. 2006, Cotner and Schooley 2011, Duggan et al. 2011, Long et al. 2011). I conducted occupancy modeling for three medium-sized mammal species with adequate data: raccoons, eastern cottontails, and coyotes (Table 2). I used single-season models in program PRESENCE 9.5 (Hines 2006) to examine relationships separately for summer and winter. Multi-season models that could evaluate turnover across seasons (MacKenzie et al. 2006) did not converge. I used a design in which each of the four camera stations at a site was treated as a spatial replicate and sampling

was conducted without replacement (Guillera-Arroita 2011). Hence, there were four surveys per site during each season.

I used a two-step approach to evaluate occupancy models (Cosentino et al. 2010, Duggan et al. 2011, Cove et al. 2012). First, I determined the most supported model for detection (p) while holding occupancy (psi) constant. The candidate set for detection included the intercept-only model [p(.)], p(Size), p(Effort), and p(Size, Effort). Then, after identifying the best detection model, I evaluated a candidate set for the occupancy covariates (Table 1) that was tailored to each species based on previous research and to address my hypotheses. The covariates combinations were limited to two to avoid overparameterization and increase the likelihood of model convergence in PRESENCE. However, not all models converged (see Tables A1, A2 for full candidate sets). Vegetation and Size_Iso were selected as occupancy covariates for all species as I expected that vegetation cover, grassland size, and degree of isolation could be important predictors of site use for an omnivore, herbivore, and predator. For raccoons, I also included Forest, Pond, and Stream as covariates as I expected negative relationships between site use by raccoons and distances to these landscape features (Newbury and Nelson 2007, Beasley et al. 2011). For cottontail rabbits, I also included Human as an occupancy covariate because of a known association with farmsteads during winter (Mankin and Warner 1999b), plus Predator because lagomorph and coyote distributions could be positively or negatively correlated (Arias-Del Razo et al. 2012). For coyotes, I also included distances to forest, for which I expected a negative relationship (Atwood et al. 2004), and distances to human structures, for which I expected a positive relationship (Gosselink et al. 2003, Magle et al. 2014). Prey was also used as an occupancy covariate for coyotes (Arias-Del Razo et al. 2012).

I evaluated models at both stages (detection and occupancy) using an information-theoretic approach (Burnham and Anderson 2002). Models with a ΔAIC value ≤ 2.0 were considered as competitive. I also considered model fit of competitive models when making inferences to avoid support of uninformative variables (Arnold 2010).

Activity of White-tailed Deer

Because naïve occupancy of white-tailed deer was high, especially in summer, occupancy modeling would not be informative. Instead, I modeled the activity of deer using the number of independent photographs (>60 min apart) as the response variable. I used a negative binomial model with a log link function and included sampling effort as an offset variable (GENMOD Procedure, SAS Institute Inc. 2013). Separate models were evaluated for each season using an information-theoretic approach (Burnham and Anderson 2002). Each candidate set included the intercept-only model plus models with Vegetation, Size_Iso, Forest, and Predator singly and in combinations with two predictors.

Seasonal Patterns

I evaluated two response variables to determine if overall use of the created grasslands by species differed between summer and winter. First, I used conditional occupancy probability for each site derived from the most supported model for each species. Second, I used photo-activity rate (DaVanon et al. 2016) that equaled the number of independent photos of each species divided by sampling effort for each site. I tested for differences in occupancy probability and photo-activity rate between seasons with the Wilcoxon Signed Rank Test (UNIVARIATE Procedure, SAS Institute Inc. 2013).

RESULTS

Eight species of mammals were encountered at varying frequencies (greatest to least): white-tailed deer, eastern cottontail, coyote, raccoon, striped skunk (*Mephitis mephitis*), Virginia opossum (*Didelphis virginiana*), American mink (*Neovison vison*), and long-tailed weasel (*Mustela frenata*) (Table 2). Of those, four species (skunk, opossum, mink, and weasel) were detected too infrequently for occupancy modeling. Despite cameras operating for a total of 5,638 days across the two seasons, I surprisingly did not capture any photographs of red fox on my restored grassland sites.

Occupancy Models

For raccoons, the best detection model in summer was p(Size). A second model, p(Size, Effort), was competitive but did not substantially improve model fit (Table 3). Detection of raccoons decreased with patch size (B = -1.048, SE = 0.464). Per-survey detection probabilities for sites averaged 0.26 (SE = 0.04). For winter, there was no strong support for any detection covariates for raccoons as the intercept-only model was ranked first (Table 4). The average per-survey detection probability for winter was 0.32 (SE = 0.12). During summer, occupancy of raccoons was best explained by a model that included distance to nearest forest (Table 3). Raccoon occupancy started to decline when distance to the nearest forest exceeded ~50 m, and occupancy was especially low when forested habitat was >400 m away (Fig. 2). The second-ranked model that also included distance to nearest pond did not improve model fit substantially (Table 3). During winter, there was less model uncertainty and raccoon occupancy was explained by Forest and Size_Iso (Table 4). Only grassland sites near forests had high

occupancy probabilities, and occupancy was higher for smaller, connected sites than for larger, isolated sites (Fig. 2).

For cottontails, the best model for detection during summer was p(Size), and the best model during winter was p(Size, Effort) (Tables 3 and 4). Detection of cottontails was related negatively to patch size in summer (B = -0.759, SE = 0.277) and winter (B = -0.477, SE = 0.237). During winter, cottontail detection also was related positively to effort (B = 0.113, SE = 0.061). Per-survey detection probabilities averaged 0.31 (SE = 0.03) for summer and 0.37 (SE = 0.02) for winter. For occupancy, the best model during summer was psi(Size_Iso) (Table 3). Site occupancy for cottontails was greater for larger, isolated grasslands than for smaller, connected grasslands (Fig 3). The intercept-only model was competitive, but the addition of Size_Iso improved model fit (Table 3). The other competitive models included Size_Iso plus one additional predictor that did not improve model fit (Table 3). For winter, the best occupancy model was psi(Vegetation). The intercept-only model was again competitive, but inclusion of Vegetation improved model fit (Table 4). Occupancy probability was 0.832 (SE = 0.173) for sites dominated by cool-season grasses, 0.643 (SE = 0.156) for mixed sites, and 0.395 (SE = 0.173) for sites dominated by warm-season grasses.

For coyotes, I did not find support for any detection covariates; the top model for detection in summer and winter was the intercept-only model (Tables 3, 4). The average per-survey detection probability was 0.12 (SE = 0.08) for summer and 0.25 (SE = 0.10) for winter. For occupancy, the best model during summer was psi(Human, Prey) (Table 3). Occupancy for coyotes was related negatively to distance to nearest human structure (B = -1.34, SE = 0.833) and to conditional occupancy of cottontail rabbits (B = -3.55, SE = 2.68) (Fig. 4). For winter, the

top model of coyote occupancy was the intercept-only model (Table 4). Other competitive models did not substantially improve model fit.

Activity of White-tailed Deer

During summer, activity of white-tailed deer based on photographic rate was best explained by a model that included distance to nearest forest (Table 5). A second-ranked model that also included Size_Iso was competitive but did not substantially improve model fit. Activity of deer was related negatively to distance to forest (B = -0.001, SE = 0.0003). During winter, the intercept-only model was ranked first (Table 5). Two models that included either Forest or Predator (coyote) were competitive but did not substantially improve model fit.

Seasonal Patterns

Based on estimates of conditional site occupancy for my most supported models (Tables 3 and 4), occupancy by raccoons changed between seasons (S = -155, $P < 0.001$, $n = 30$), decreasing from summer to winter (Fig. 5). However, site occupancy for cottontail rabbits (S = 48.5, $P = 0.198$, $n = 30$) and coyotes (S = -5.5, $P = 0.892$, $n = 30$) did not differ between seasons.

Based on photograph rate, activity of raccoons (S = -12, $P = 0.384$, $n = 30$) and coyotes (S = 5, $P = 0.821$, $n = 30$) did not vary between seasons. In contrast, activity of cottontails (S = 56, $P = 0.013$, $n = 30$) and white-tailed deer (S = 119, $P = 0.012$, $n = 30$) increased on restored grasslands during the winter (Fig. 5).

DISCUSSION

I applied camera trapping to gain rare insights into how mammals used restored grasslands in Midwestern landscapes dominated by agriculture. I detected eight native species of medium and large mammals. Thus, grasslands created under the CRP and SAFE programs provide habitat for these species as well as other, more-studied vertebrates such as small mammals (Mulligan et al. 2013) and birds (Clark and Bogenschutz 1999, McCoy et al. 1999). Use of grasslands differed between summer and winter for three of the four species examined in detail, which suggests the dynamic nature of the agricultural matrix was consequential. Landscape context, such as distance to other critical habitats and connectivity among restored sites, also had strong effects on restoration outcomes. Historically, restoration assessments have focused on local habitat quality and ignored landscape context (Brudvig 2011). My results are consistent with those of Mulligan et al. (2013), however, who found landscape context affected colonization rates of newly created grasslands by small mammals in my region.

Landscape context had especially clear influences on site occupancy by raccoons. The most supported models for raccoon occupancy in both seasons included distance to nearest forest. This result was expected as raccoons are known to favor forested habitats (Beasley and Rhodes 2010, Beasley et al. 2011), especially for denning (Henner et al. 2004). However, there were seasonal nuances to this main effect that were likely related to the harvesting of crops in the matrix. During summer, occupancy of grasslands by raccoons was higher, and occupancy probabilities were moderate when sites were 55 to 400 m from forest (Fig. 2). During winter, when the matrix was bare of crops, there was a much sharper reduction in occupancy probability with distance to forest. Moreover, raccoons were more likely to use sites that were well connected to other grasslands during winter (Fig. 2), presumably because the cover encouraged

movements among nearby grasslands and from nearby forest. Because Size_Iso is a synthetic variable that reflects both patch isolation and patch size, raccoons could also have used the smaller grasslands more often because they had more edge habitat, which raccoons prefer (Renfrew and Ribic 2003, Renfrew et al. 2005, Barding and Nelson 2008).

The increased use of restored grasslands by raccoons during summer coincides with the nesting of grassland bird species. Many bird species associated with grasslands in North America have declined (Knopf 1994, Herkert 1995), and new grasslands created under federal programs may benefit some species (Herkert 2009). Given the potential importance of raccoons as nest predators (Heske et al. 1999, Schmidt 2003, Lyons et al. 2015), I recommend that managers concerned with habitat restoration for grassland birds should focus on sites >400 m from forests. Currently, enrollment in the SAFE program is restricted to designated SAFE areas and includes basic eligibility requirements (USDA 2008), but the location of potential SAFE grasslands relative to forests is not a consideration for enrollment.

My hypothesis that the herbivorous prey species (cottontails and deer) would prefer cool-season grasslands that provide denser hiding cover (McCoy et al. 2001) over warm-season grasslands received only limited support. A positive association was found between site occupancy for cottontails and dominance of cool-season grasses during winter only. Evidently, vegetation type is not as important during summer when crops can provide extra cover. For white-tailed deer, which should primarily be concerned with fawn predation, vegetation type did not affect photo-activity rate in either season, and only distance to the nearest forest (Nixon et al. 1991, 2012) predicted activity during summer. Overall, I did not detect any negative consequences of vegetation dominated by cool-season grasses, typically smooth brome, instead of warm-season grasses. This outcome is consistent with research for small mammals on newly

created SAFE grasslands (Mulligan et al. 2013). Likewise, Duggan et al. (2011) found that smooth brome grasslands could function as suitable habitat for Franklin's ground squirrel (*Poliocitellus franklinii*), often considered a prairie-obligate species. Clearly, seeding with native warm-season species remains preferable from a floristics standpoint, and other animal taxa may be more discriminating and prefer warm-season grasslands.

Both cottontails and white-tailed deer substantially increased their activity on my grassland sites during winter based on photo-activity rate (Fig. 5). These species likely spent more time in the restored grasslands partly due to the drastic reduction in vegetative cover in the surrounding agricultural matrix after harvest. Radiomarked cottontails in central Illinois reduced their home ranges from 11.8 ha during the crop growing season to 6.2 ha during the non-growing season (Mankin and Warner 1999b). The seasonal loss of cover from annual crops should concentrate prey species on patches of suitable habitat such as our created grasslands.

I found no evidence, however, that coyotes were spatially tracking one of their key prey species, eastern cottontails. The occupancy probability and photo-activity rate of coyotes did not change between seasons. Moreover, even though 'Prey' was in the top model for coyote occupancy during summer, the relationship was negative, indicating coyotes were less likely to occupy sites with cottontails. This result was consistent with patterns of habitat use for coyotes and desert lagomorphs (Ariaz-Del Razo et al. 2012). One explanation for this discordance is that predators might spend more time hunting in areas where prey are less common but more vulnerable (Ariaz-Del Razo et al. 2012). Coyote occupancy during summer also was higher when restoration sites were closer to human structures. This result is counter to my hypothesis based on the notion that coyotes avoid humans (Gosselink et al. 2003, Magle et al. 2014), and I have no explanation for this surprising association. For winter, the intercept-only model was

most supported for coyote occupancy. In general, the factors affecting the spatial distribution of coyotes within my patchy landscapes were not well resolved (see also Cove et al. 2012).

I expected a negative pattern of occurrence between red foxes and coyotes due to competitive exclusion and intraguild predation (Lavin et al. 2003, Gosselink et al. 2006). Although red foxes are a species associated with open habitat, I detected no red foxes on my restored grasslands despite 5,638 camera days of sampling over two seasons. My camera trapping was intensive enough to record secretive mustelids like long-tailed weasels and American mink. These results suggest red foxes are now quite rare in rural areas of central Illinois. Foxes may occur more often in habitats near people (Goad et al. 2014, Lesmeister et al. 2015). For instance, foxes have found refuge from coyotes near farmsteads in rural areas of central Illinois (Gosselink et al. 2006). In my study, however, an avoidance of farmsteads by coyotes was not evident. Monitoring efforts are needed to determine the status of red foxes outside of urban areas more broadly in the Midwest region.

My study illustrates how camera trapping can improve assessments of restoration outcomes by expanding focal groups to include medium and large mammals. My results demonstrate that landscape context can strongly affect occupancy of restored grasslands by mammals in a highly modified landscape. Species occurrences were associated with grassland size and isolation, distances to human structures, and distances to nearest forest. Some of these outcomes can assist land managers in selecting land parcels to enroll in habitat restoration programs (e.g., to reduce the chance of nest predation by raccoons). Future research should focus on the mechanisms of habitat selection, and consequences for fitness, for mammals using created grasslands in dynamic agroecosystems.

TABLES AND FIGURES

Table 1. Covariates used in estimating detection and occupancy probabilities for mammals on restored grasslands in Illinois. Medians and ranges are provided for raw data; landscape covariates (distances to features) were ln-transformed for occupancy modeling.

Covariate	Description	Median	Range
Size	Size of focal grassland (ha)	28.7	1 - 256
Effort (S)	No. days cameras were active in summer	28	14 - 28
Effort (W)	No. days cameras were active in winter	28	15 - 28
Vegetation	Ordinal designation for dominant grasses: Cool-season (1), Mixed (2), or Warm-season (3)	_	_
Grassland	Distance to nearest grassland (m)	35.0	6 - 4723
Human	Distance to nearest human structure (m)	79.5	0 - 1139
Forest	Distance to nearest forest (m)	91.5	0 - 1500
Stream	Distance to nearest stream (m)	101.5	0 - 2260
Pond	Distance to nearest pond (m)	192.5	0 - 2009
Prey (S)	Conditional occupancy probability for cottontail rabbits during summer	0.48	0.01 - 1
Prey (W)	Conditional occupancy probability for cottontail rabbits during winter	0.63	0.07 - 1
Predator (S)	Conditional occupancy probability for coyotes during summer	0.64	0.04 - 1
Predator (W)	Conditional occupancy probability for coyotes during winter	0.32	0.26 - 1

Table 2. Naïve occupancy (no. sites with detections/30 total sites) and number of independent photographs (>60 min apart) of all mammals detected by camera traps during summer and winter in central Illinois (2014-2015).

	Summer		**Winter**	
Species	**Naïve occupancy**	**No. photos**	**Naïve occupancy**	**No. photos**
White-tailed deer **(*Odocoileus virginianus*)**	0.97	117	0.77	203
Eastern cottontail **(*Sylvilagus floridanus*)**	0.30	131	0.47	360
Coyote **(*Canis latrans*)**	0.33	18	0.33	16
Raccoon **(*Procyon lotor*)**	0.27	48	0.20	17
Striped skunk **(*Mephitis mephitis*)**	0.23	9	0.20	22
Virginia opossum **(*Didelphis virginiana*)**	0.10	3	0.20	11
American mink **(*Neovison vison*)**	0.10	2	0.00	0
Long-tailed weasel **(*Mustela frenata*)**	0.00	0	0.03	2

Table 3. Model selection statistics for detection and occupancy for raccoons, cottontails, and coyotes during summer 2014 in central Illinois. Occupancy models presented include those with $\Delta AIC \leq 2$ plus the intercept-only model. Full candidate sets for occupancy are in the Appendix (Table A1). Covariates are defined in Table 1. ΔAIC = difference between model AIC and AIC for top model, w_i = Akaike weight, K = no. estimable parameters, and -2LogLike = twice the negative log-likelihood.

Species	**Parameter**	**Model**	**ΔAIC**	w_i	**K**	**-2*LogLike**
Raccoon	Detection	psi(.), p(Size)	0	0.493	3	70.82
		psi(.), p(Size, Effort)	0.91	0.313	4	69.73
		psi(.), p(.)	2.76	0.124	2	75.58
		psi(.) ,p(Effort)	3.88	0.071	3	74.70
	Occupancy	psi(Forest), p(Size)	0	0.233	4	67.49
		psi(Forest, Pond), p(Size)	1.26	0.124	5	66.75
		psi(.), p(Size)	1.33	0.120	3	70.82
		psi(Forest, Stream), p(Size)	1.92	0.089	5	67.41
		psi(.), p(.)	4.09	0.0293	2	75.58
Cottontail	Detection	psi(.), p(Size)	0	0.532	3	77.61
		psi(.), p(Size, Effort)	1.52	0.249	4	77.13
		psi(.), p(.)	2.97	0.121	2	82.58
		psi(.), p(Effort)	3.37	0.099	3	80.98
	Occupancy	psi(Size_Iso), p(Size)	0	0.253	4	74.73
		psi(.), p(Size)	0.88	0.163	3	77.61
		psi(Size_Iso, Vegetation), p(Size)	1.91	0.097	5	74.64
		psi(Size_Iso, Predator), p(Size)	1.97	0.095	5	74.70
		psi(Size_Iso, Human), p(Size)	2	0.093	5	74.73
		psi(.), p(.)	3.85	0.036	2	82.58
Coyote	Detection[a]	psi(.), p(.)	0	0.584	2	77.73
		psi(.), p(Size)	0.68	0.416	3	76.41
	Occupancy	psi(Human, Prey), p(.)	0	0.301	4	71.34
		psi(Human), p(.)	0.73	0.209	3	74.07
		psi(.), p(.)	2.39	0.091	2	77.73

[a] Detection models psi(.),p(Effort) and psi(.), p(Size, Effort) did not converge.

Table 4. Model selection statistics for detection and occupancy for raccoons, cottontails, and coyotes during winter 2014-2015 in central Illinois. Occupancy models presented include those with $\Delta AIC \leq 2$ plus the intercept-only model. Full candidate sets for occupancy are in the Appendix (Table A2). Covariates are defined in Table 1. ΔAIC = difference between model AIC and AIC for top model, w_i = Akaike weight, K = no. estimable parameters, and -2LogLike = twice the negative log-likelihood.

Species	Parameter	Model	ΔAIC	wi	K	-2*LogLike
Raccoon	Detection	psi(.), p(.)	0	0.368	2	59.58
		psi(.), p(Size)	0.2	0.333	3	57.78
		psi(.), p(Size, Effort)	1.77	0.152	4	57.35
		psi(.), p(Effort)	1.83	0.147	3	59.41
	Occupancy	psi(Size_Iso, Forest), p(.)	0	0.506	4	50.05
		psi(.), p(.)	5.53	0.032	2	59.58
Cottontail	Detection	psi(.), p(Size, Effort)	0	0.470	4	100.06
		psi(.), p(Effort)	1.11	0.270	3	103.17
		psi(.), p(Size)	2.28	0.150	3	104.34
		psi(.), p(.)	2.91	0.110	2	106.97
	Occupancy	psi(Vegetation), p(Size, Effort)	0	0.245	5	97.57
		psi(.), p(Size, Effort)	0.49	0.192	4	100.06
		psi(Human), p(Size, Effort)	1.32	0.127	5	98.89
		psi(Vegetation, Predator), p(Size, Effort)	1.88	0.096	6	97.45
		psi(Predator), p(Size, Effort)	1.9	0.095	5	99.47
		psi(.), p(.)	3.4	0.043	2	106.97
Coyote	Detection	psi(.), p(.)	0	0.427	2	80.17
		psi(.), p(Size)	0.7	0.301	3	78.87
		psi(.), p(Effort)	1.94	0.162	3	80.11
		psi(.), p(Size, Effort)	2.7	0.111	4	78.87
	Occupancy	psi(.), p(.)	0	0.204	2	80.17
		psi(Forest), p(.)	1.47	0.098	3	79.64
		psi(Size_Iso), p(.)	1.7	0.087	3	79.87
		psi(Human), p(.)	1.7	0.087	3	79.87
		psi(Prey), p(.)	1.79	0.083	3	79.96
		psi(Vegetation), p(.)	1.92	0.078	3	80.09

Table 5. Model selection statistics for negative binomial models for activity of white-tailed deer (photographic rate) during summer and winter in central Illinois (2014-2015). Covariates are defined in Table 1. ΔAICc = difference between model AICc and AICc for top model, w_i = Akaike weight, K = no. estimable parameters, and LL = log-likelihood.

Season	**Model**	**ΔAIC_c**	**w_i**	**K**	**LL**
Summer	Forest	0	0.483	3	54.19
	Forest, Size_Iso	1.767	0.200	4	54.60
	Forest, Predator	2.267	0.155	4	54.20
	Forest, Vegetation	2.547	0.135	4	54.21
	Intercept-only	7.666	0.010	2	49.07
	Size_Iso	9.005	0.005	3	49.64
	Vegetation	9.824	0.004	3	49.23
	Predator	10.143	0.003	3	49.07
	Size_Iso, Predator	10.895	0.002	4	49.64
	Vegetation, Size_Iso	11.477	0.002	4	49.74
	Vegetation, Predator	12.494	0.001	4	49.24
Winter	Intercept-only	0	0.252	2	242.13
	Forest	0.512	0.195	3	243.11
	Predator	1.575	0.115	3	242.58
	Size_Iso	2.2	0.084	3	242.47
	Vegetation	2.395	0.076	3	242.17
	Forest, Predator	2.804	0.062	4	243.51
	Forest, Vegetation	3.095	0.054	4	243.16
	Forest, Size_Iso	3.097	0.054	4	243.16
	Vegetation, Predator	3.449	0.045	4	242.98
	Size_Iso, Predator	3.588	0.042	4	242.72
	Vegetation, Size_Iso	4.761	0.023	4	242.32

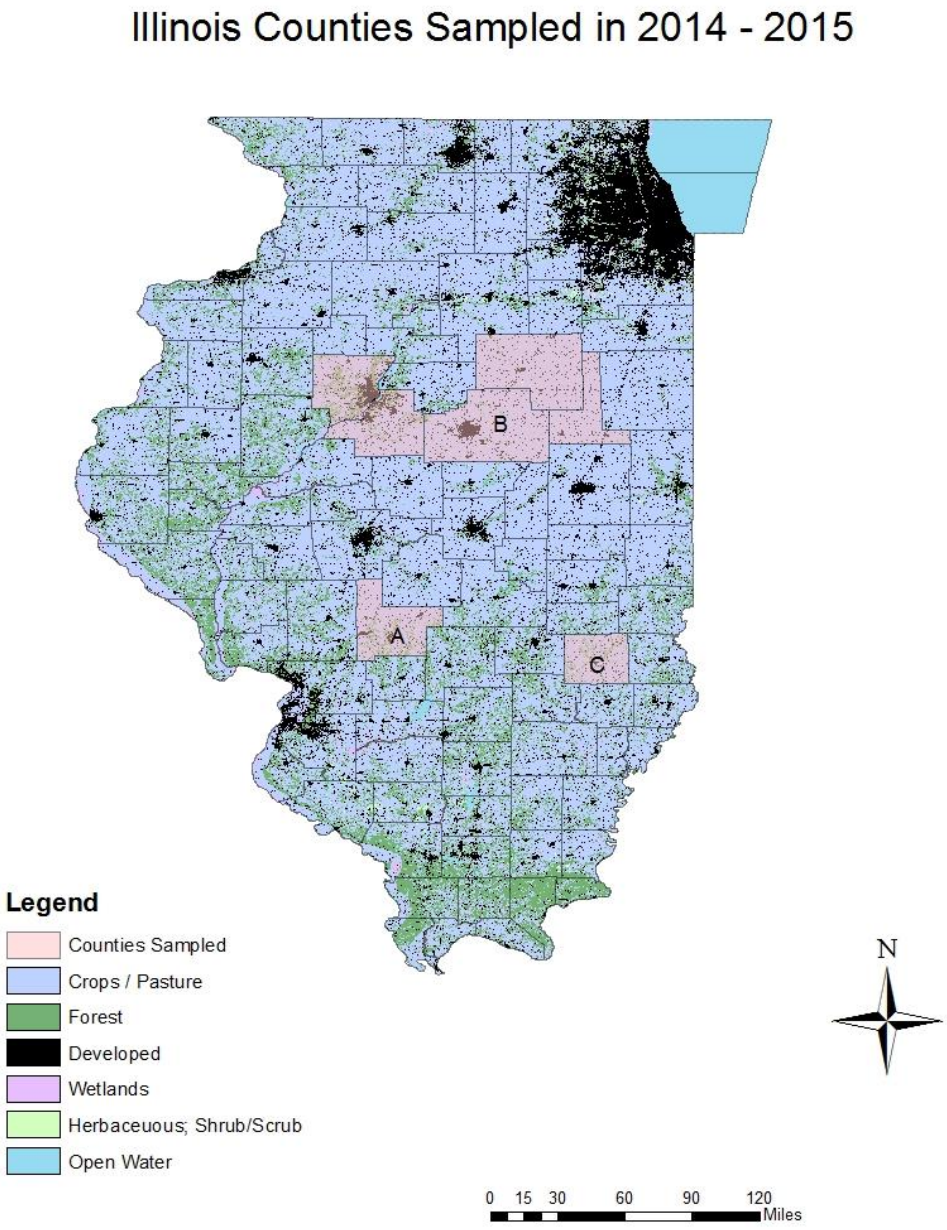

Figure 1. Map of Illinois showing counties where sampling was conducted for site occupancy by mammals on restored grassland (2014-2015). Counties include Ford, Jasper, Livingston, McLean, Montgomery, Peoria, and Tazewell. The number of sites sampled in each group: A = 3, B = 23, and C = 4.

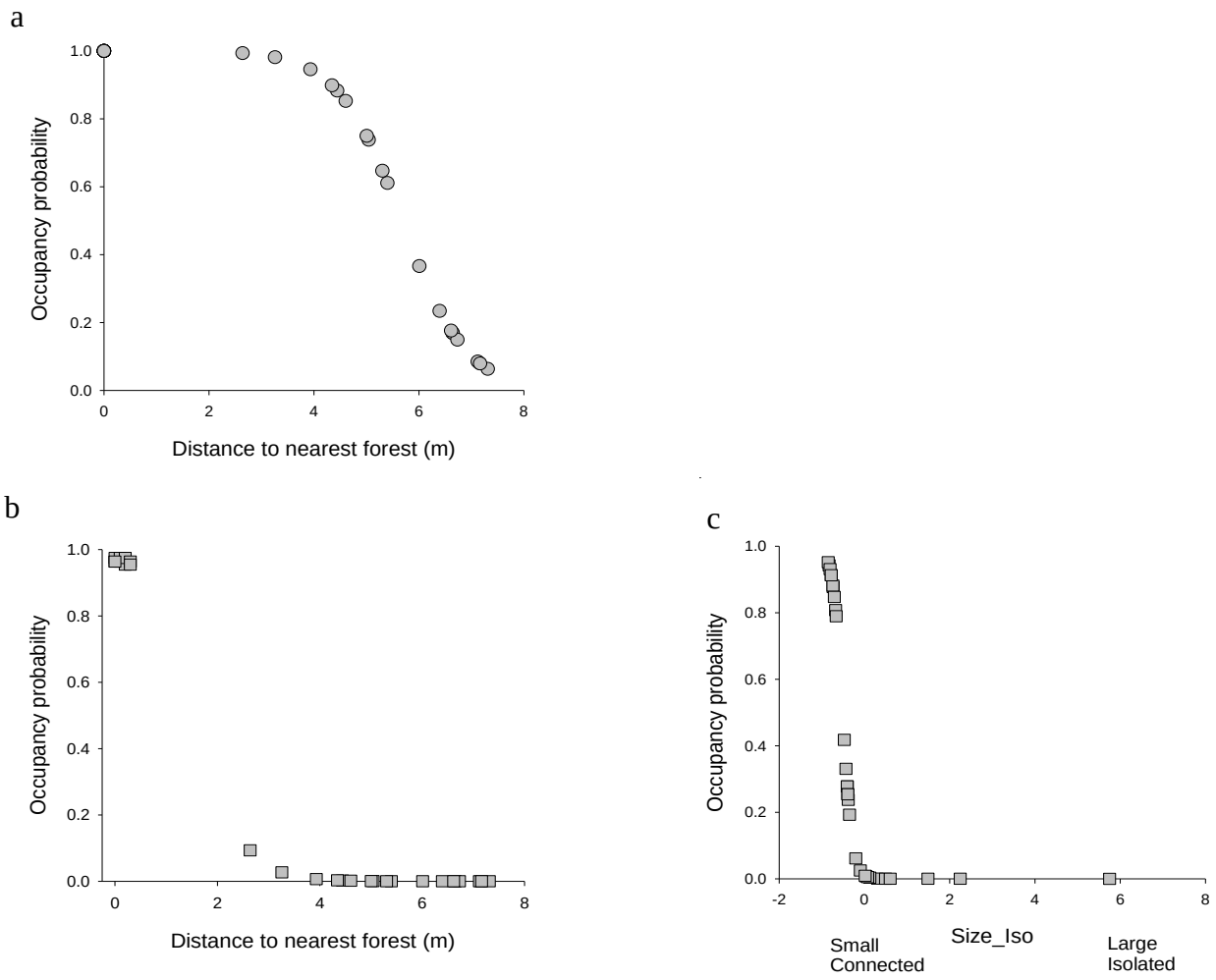

Figure 2. Occupancy of restored grasslands by raccoons during summer (a) and winter (b, c) in central Illinois (2014-2015). Distances to nearest forest were ln-transformed. Size_Iso is a synthetic variable that ranges from small and connected sites to large and isolated sites. For winter, predicted occupancy probability is shown with the other covariate held to its mean value.

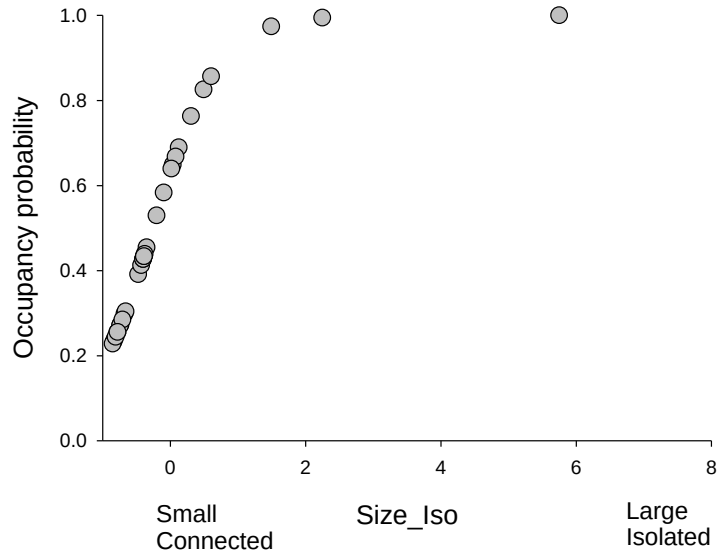

Figure 3. Occupancy probabilities of eastern cottontails on restored grasslands during summer in central Illinois (2014). Size_Iso is a synthetic variable that ranges from smaller, more connected sites to larger, more isolated sites.

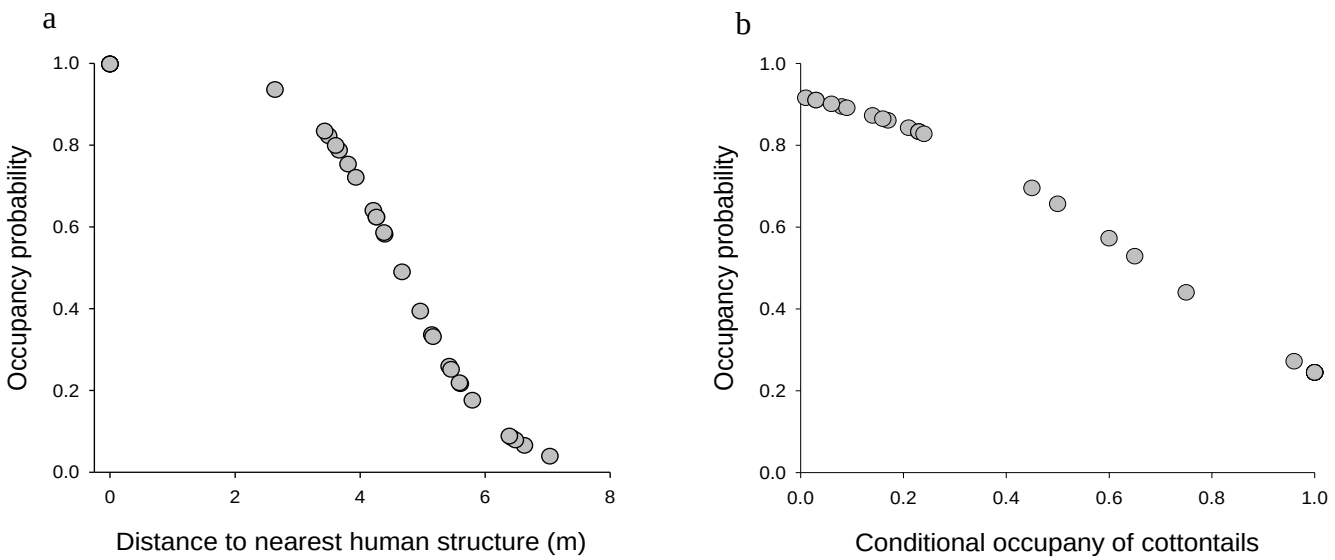

Figure 4. Occupancy probabilities of coyotes on restored grasslands during summer in central Illinois (2014). (a) Distance to nearest human structure was ln-transformed. (b) The conditional occupancy probabilities of cottontails are from the top model (see Table 3). For both panels, predicted occupancy probability is shown with the other covariate held to its mean value.

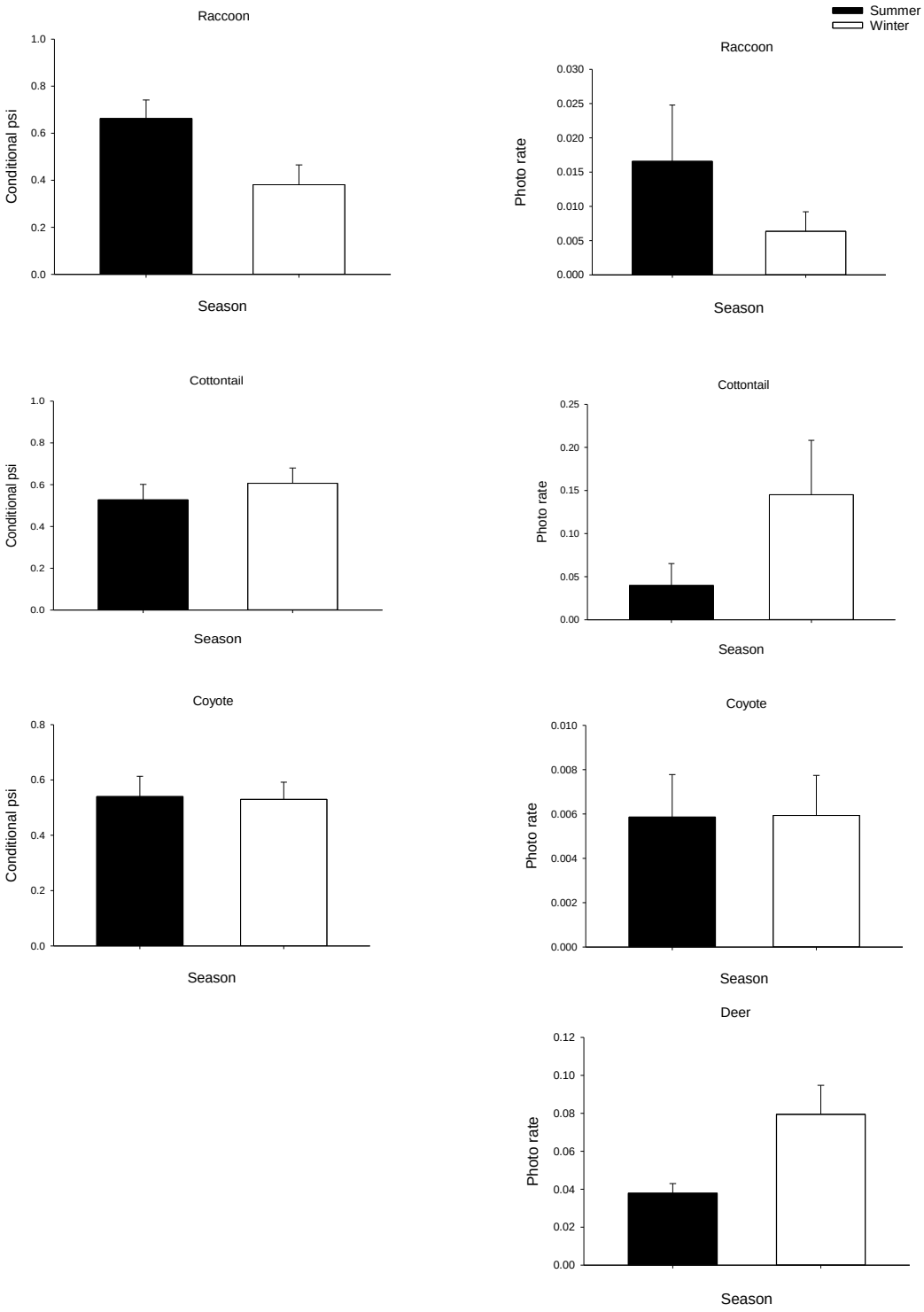

Figure 5. Seasonal patterns for use of restored grassland by raccoons, eastern cottontails, coyotes, and white-tailed deer in central Illinois (2014-2015). The left panel is conditional occupancy; the right panel is photo-activity rate (no. independent photographs/sampling effort). Bars are means (+1 SE).

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APPENDIX

Table 6. Model selection statistics for occupancy models for raccoons, cottontails, and coyotes during summer 2014 in central Illinois. ΔAIC = difference between model AIC and AIC for top model, w_i = Akaike weight, K = no. estimable parameters, and -2LogLike = twice the negative log-likelihood.

Species	Model	ΔAIC	w_i	K	-2*LogLike
Raccoon	psi(Forest), p(Size)	0	0.2334	4	67.49
	psi(Forest, Pond), p(Size)	1.26	0.1243	5	66.75
	psi(.), p(Size)	1.33	0.12	3	70.82
	psi(Forest, Stream), p(Size)	1.92	0.0894	5	67.41
	psi(Pond), p(Size)	2.15	0.0797	4	69.64
	psi(Vegetation), p(Size)	2.35	0.0721	4	69.84
	psi(Size_Iso), p(Size)	3.11	0.0493	4	70.6
	psi(Vegetation, Pond), p(Size)	3.25	0.046	5	68.74
	psi(Stream), p(Size)	3.32	0.0444	4	70.81
	psi(Size_Iso, Vegetation), p(Size)	3.94	0.0326	5	69.43
	psi(Size_Iso, Pond), p(Size)	3.94	0.0326	5	69.43
	psi(Stream, Pond), p(Size)	4.03	0.0311	5	69.52
Cottontail	psi(Size_Iso), p(Size)	0	0.2532	4	74.73
	psi(.), p(Size)	0.88	0.1631	3	77.61
	psi(Size_Iso, Vegetation), p(Size)	1.91	0.0974	5	74.64
	psi(Size_Iso, Predator), p(Size)	1.97	0.0945	5	74.7
	psi(Size_Iso, Human), p(Size)	2	0.0931	5	74.73
	psi(Human), p(Size)	2.26	0.0818	4	76.99
	psi(Vegetation), p(Size)	2.86	0.0606	4	77.59
	psi(Predator), p(Size)	2.88	0.06	4	77.61
	psi(Human, Predator), p(Size)	3.54	0.0431	5	76.27
	psi(.),p(.)	3.85	0.0356	2	82.58
	psi(Vegetation, Human), p(Size)	4.21	0.0308	5	76.94
	psi(Vegetation, Predator), p(Size)	4.86	0.0223	5	77.59
Coyote	psi(Human, Prey), p(.)	0	0.3005	4	71.34
	psi(Human), p(.)	0.73	0.2086	3	74.07
	psi(.), p(.)	2.39	0.091	2	77.73
	psi(Vegetation, Human), p(.)	2.66	0.0795	4	74
	psi(Size_Iso), p(.)	2.7	0.0779	3	76.04
	psi(Forest, Human), p(.)	2.71	0.0775	4	74.05
	psi(Vegetation), p(.)	4.08	0.0391	3	77.42
	psi(Prey), p(.)	4.34	0.0343	3	77.68
	psi(Forest), p(.)	4.35	0.0341	3	77.69
	psi(Size_Iso, Prey), p(.)	4.7	0.0287	4	76.04

Table 7. Model selection statistics for occupancy models for raccoons, cottontails, and coyotes during winter 2014-2015 in central Illinois. ΔAIC = difference between model AIC and AIC for top model, w_i = Akaike weight, K = no. estimable parameters, and -2LogLike = twice the negative log-likelihood.

Species	Model	ΔAIC	w_i	K	-2*LogLike
Raccoon	psi(Size_Iso, Forest), p(.)	0	0.5059	4	50.05
	psi(Forest), p(.)	2.72	0.1298	3	54.77
	psi(Forest, Stream), p(.)	3.32	0.0962	4	53.37
	psi(Vegetation, Stream), p(.)	4.51	0.0531	4	54.56
	psi(Vegetation), p(.)	4.78	0.0464	3	56.83
	psi(.), p(.)	5.53	0.0319	2	59.58
	psi(Size_Iso, Vegetation), p(.)	5.86	0.027	4	55.91
	psi(Stream), p(.)	6.07	0.0243	3	58.12
	psi(Size_Iso, Stream), p(.)	6.31	0.0216	4	56.36
	psi(Size_Iso), p(.)	6.6	0.0187	3	58.65
Cottontail	psi(Vegetation), p(Size, Effort)	0	0.2454	5	97.57
	psi(.), p(Size, Effort)	0.49	0.1921	4	100.06
	psi(Human), p(Size, Effort)	1.32	0.1268	5	98.89
	psi(Vegetation, Predator), p(Size, Effort)	1.88	0.0959	6	97.45
	psi(Predator), p(Size, Effort)	1.9	0.0949	5	99.47
	psi(Human, Predator), p(Size, Effort)	2.32	0.0769	6	97.89
	psi(Size_Iso), p(Size, Effort)	2.46	0.0717	5	100.03
	psi(Size_Iso, Human), p(Size, Effort)	2.78	0.0611	6	98.35
	psi(.), p(.)	3.4	0.0429	2	106.97
Coyote	psi(.), p(.)	0	0.2042	2	80.17
	psi(Forest), p(.)	1.47	0.0979	3	79.64
	psi(Size_Iso), p(.)	1.7	0.0873	3	79.87
	psi(Human), p(.)	1.7	0.0873	3	79.87
	psi(Prey), p(.)	1.79	0.0834	3	79.96
	psi(Vegetation), p(.)	1.92	0.0782	3	80.09
	psi(Forest, Human), p(.)	3.14	0.0425	4	79.31
	psi(Size_Iso, Forest), p(.)	3.14	0.0425	4	79.31
	psi(Size_Iso, Prey), p(.)	3.36	0.0381	4	79.53
	psi(Human, Prey), p(.)	3.36	0.0381	4	79.53
	psi(Forest, Prey), p(.)	3.4	0.0373	4	79.57
	psi(Vegetation, Forest), p(.)	3.47	0.036	4	79.64
	psi(Vegetation, Human), p(.)	3.7	0.0321	4	79.87
	psi(Size_Iso, Human), p(.)	3.7	0.0321	4	79.87
	psi(Size_Iso, Vegetation), p(.)	3.7	0.0321	4	79.87